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# Pitfall trap sampling bias depends on body mass, temperature, and trap number: insights from an individual-based model

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**Abstract.** The diversity and community composition of ground arthropods is routinely analyzed by pitfall trap sampling, which is a cost- and time-effective method to gather large numbers of replicates but also known to generate data that are biased by species-specific differences in locomotory activity. Previous studies have looked at factors that influence the sampling bias. These studies, however, were limited to one or few species and did rarely quantify how the species-specific sampling bias shapes community-level diversity metrics. In this study, we systematically quantify the species-specific and community-level sampling bias with an allometric individual-based model that simulates movement and pitfall sampling of 10 generic ground arthropod species differing in body mass. We perform multiple simulation experiments covering different scenarios of pitfall trap number, spatial trap arrangement, temperature, and population density. We show that the sampling bias decreased strongly with increasing body mass, temperature, and pitfall trap number, while population density had no effect and trap arrangement only had little effect. The average movement speed of a species in the field integrates body mass and temperature effects and could be used to derive reliable estimates of absolute species abundance. We demonstrate how unbiased relative species abundance can be derived using correction factors that need only information on species body mass. We find that community-level diversity metrics are sensitive to the particular community structure, namely the relation between body mass and relative abundance across species. Generally, pitfall trap sampling flattens the rank-abundance distribution and leads to overestimations of ground arthropod Shannon diversity. We conclude that the correction of the species-specific pitfall trap sampling bias is necessary for the reliability of conclusions drawn from ground arthropod field studies. We propose bias correction is a manageable task using either body mass to derive unbiased relative abundance or the average speed to derive reliable estimates of absolute abundance from pitfall trap sampling.

**Key words:** allometric relationship; correction factor; ground-dwelling arthropod; individual-based model; pitfall trap; sampling bias; virtual ecologist.

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## Introduction

Quantification of animal densities in the field is essential to understand impacts of climate and land-use change on community biodiversity (Iknayan et al. 2014). This is particularly true for the large group of ground-dwelling arthropods (here referred to as ground arthropods) as they are highly responsive to environmental changes and influence a large number of ecosystem functions such as predation and decomposition (Finke and Snyder 2010, Chaplin-Kramer et al. 2011, Prather et al. 2013). The passive sampling of ground arthropods with pitfall traps, that is, small containers buried to the ground, was used in many biodiversity and conservation studies across the recent decades and is still being used today (Greenslade 1964, Zhao et al. 2013, Brown and Matthews 2016). The benefits of pitfall trap sampling are its time efficiency and the high probability to detect rare and nocturnal species that other methods might miss (Spence and Niemelä 1994, Lang 2000, Cardoso et al. 2008). There are, however, a number of factors that produce biases in the species abundance estimated from pitfall trap sampling affecting the species-specific sampling efficiency. Sampling bias has been shown to depend on, for example, population density and factors that change locomotory activity such as body mass and ambient temperature (Halsall and Wratten 1988, Mommertz et al. 1996, Lang 2000, Perner and Schueler 2004, Woodcock 2005, Saska et al. 2013, Brown and Matthews 2016). Hence, the sampling bias likely varies across species and environmental conditions hampering field experiments to get insight into how environmental changes affect arthropod communities.

Population density of ground arthropods varies across years and habitats; though, limited knowledge exists about how accurate the sampled density reflects variation in the real density (Collins et al. 2003, Hutchison 2007, Woodcock 2005). Variation in the ambient temperature can produce considerable bias in pitfall sampling because the locomotory activity of most ground arthropods varies with ambient temperature, and sampled densities are proportional to locomotory activity (Thomas et al. 1998, Woodcock 2005). The number of pitfall traps and their spatial arrangement have been shown to strongly influence the reliability of sampled densities for estimations of real densities (Scheller 1984, Parmenter and MacMahon 1989, Perner 2003, Zhao et al. 2013). Moreover, only limited knowledge exists about how the species-specific sampling bias may impact community-level metrics considering variation in community structure across ecosystems, such as the distribution of species body masses across the abundance ranks (Topping and Sunderland 1992).

Previous empirical studies that aimed at analyzing the species-specific pitfall sampling bias and providing recommendations for statistical corrections focused on only one or few of the confounding factors, mostly covering small ranges of parameter values (e.g., Greenslade 1964, Spence and Niemelä 1994, Thomas et al. 1998, Work et al. 2002). Today, there is only fragmented knowledge about how the pitfall trap sampling bias affects both sampled population densities and estimated metrics of community diversity across different combinations of, for example, trap number, trap arrangement, species body mass, community structure, and climatic conditions.

Computational simulations can reduce knowledge gaps by simulating ground arthropods movement and sampling across many factors, such as trap number, trap arrangement, and ambient temperature (Perner and Schueler 2004, Pyke 2015). Nevertheless, the simulation of large numbers of different ground arthropod species is limited by the great parameterization effort necessary to model realistic movement of many species. This parameterization effort, consequently, also proved to be a methodological frontier to analyses of how the species-specific sampling bias may affect community-level metrics, such as the species rank-abundance distribution (RAD) and Shannon diversity (McGill et al. 2007, Locey and White 2013). Recent simulation studies simulated the movement of one or two ground arthropod species specifically emphasizing the impact of the spatial arrangement of traps on efficiency and reliability of sampled densities (Crist and Wiens 1995, Perner and Schueler 2004, Ellis and Bedward 2014). These studies simulated the movement of virtual individuals in a homogeneous two-dimensional landscape. The virtually sampled population densities were compared to the simulated densities to validate the efficiency of

trap arrangements and reveal the species-specific sampling bias. The basic idea behind these modeling exercises was to simulate data and observer models to mimic real species and their sampling, being in control of all conditions and aware of any sampling bias. This basic idea was formalized by Zurell et al. (2010) as evaluation framework for the assessment of sampling protocols and analysis in ecology, naming it the "virtual ecologist" approach. When applying the virtual ecologist approach to ground arthropod pitfall sampling, the effectiveness of sampling designs can be rigorously tested against a simulated known truth, providing a strong basis for future field experiments and empirical validation.

Here, we apply the virtual ecologist approach to investigate the pitfall sampling bias at the species and the community level. We developed an individual-based model for simulating the movement and pitfall trap sampling across 10 "generic species" of actively hunting ground arthropods that differ in body mass ranging from 1 to 330 mg. We parameterized the simulated ground arthropod movement applying allometric relationships and empirical sampling data integrating knowledge about temperature and body mass effects on arthropod movement (e.g., Klazenga and Devries 1994, Thomas et al. 1998, Hurlbert et al. 2008). We conducted 840 simulation experiments to identify how (1) the species-specific sampling bias, (2) the observed RAD, and (3) the estimated community diversity metrics are affected by (i) trap number (1, 2, 4, 8, and 12), (ii) trap arrangement (Appendix S3: Fig. S1), (iii) body mass, (iv) body temperature (15–30°C), (v) population density (0.15–8 individuals/$m^2$), and (vi) community structure (sequence of body masses across the abundance ranks). We aimed for simple ways to retrieve correction factors that would allow reasonable estimates of unbiased relative and absolute species densities from pitfall trap sampling.

## Methods

The present study used an allometric individual-based model to simulate the movement of individuals across 10 generic species of actively hunting ground arthropods. The simulated individuals were "virtually" sampled applying different pitfall trap numbers and spatial arrangements. The 10 generic species (here referred to as species) differed only in body mass; that is, no specific real species were modeled. We applied an empirical relationship between movement speed and body mass plus body temperature to adequately simulate the species-specific movement speed (Hurlbert et al. 2008). Additionally, movement parameters across species were improved and validated using a different set of published empirical data (Klazenga and Devries 1994, Thomas et al. 1998, Byers 2001).

The model predicted the number of individuals per species sampled by pitfall traps across 14 simulation days. We defined the sampling bias as the species-specific proportion of simulated individuals that were *not* sampled. Multiple simulation experiments were conducted modeling all 10 species across various combinations of trap number, trap arrangement, population density, and body temperature.

The following sections describe the simulation model accordingly to the ODD protocol (overview, design concepts, and details; Grimm et al. 2010), the simulation experiments with the particular parameter values used, and the data analysis. The parameterization and validation of arthropod movement as well as the local sensitivity analysis are covered in Appendices S1 and S2. The model was implemented using the programming language C++.

### *Model description*

*Purpose.*—The purpose of the model is to predict the number of individuals per species that are sampled by pitfall traps during the simulation experiment. The simulation experiments enable reliable estimations of the pitfall trap sampling bias for various parameter combinations of body mass, population density, body temperature, trap number, and trap arrangement, for which no empirical data exist. The sampling of ground arthropod individuals is not imposed, but emerges from the movement of individuals within the simulated area. The model simulates movement patterns of arthropod species that are actively hunting at the ground.

*State variables and scales.*—Model entities were individuals resembling actively hunting ground arthropods of a distinct class of body mass. All state variables characterizing an individual are

listed in Table 1. During one simulation experiment, the body mass and the body temperature were fixed, but individuals were different in their position in the simulated area, their direction of movement, and the mortality status. Species-specific activity periods were simplified such that all individuals across all species were active at the same time. Body temperature of each individual was assumed to exceed ambient temperature by 8°C simplifying effects from variation in microhabitat conditions (Casey 1976, Morgan 1985).

The simulated, homogeneous, and featureless area spanned 20 × 20 m with a resolution of 1 × 1 cm, resulting in a grid of 2000 × 2000 cells. We assumed that the simulated area is enclosed in a very large field with a population density equal to the density within the simulated area (Perner and Schueler 2004). The boundaries of the area were simulated as permeable allowing individuals to leave and enter the simulated area. In the simulation experiments, an individual that left the area immediately re-entered the area at the opposite (i.e., the area was simulated as torus). One time step in the model was a discrete event corresponding to 10 s. Simulation experiments were run for 14 d, totaling 120,960 time steps, corresponding to the sampling period often used in empirical studies (e.g., Topping and Sunderland 1992, Diekotter et al. 2010). The pitfall traps had a diameter of 5 cm and were located according to the specific trap number and trap arrangement (Appendix S3: Figs. S1, S2).

*Process overview and scheduling*.—At each time step, the processes presented in Fig. 1 were computed in the given order starting with "activity." Per time step the individuals were processed one by one using always the same sequence. Changes in state variables were updated immediately. All processes are briefly described below and in detail in the "submodels" section.

1. Activity: Whether an individual was active or not depended on the predefined activity period, which spanned eight consecutive hours and was assumed to be equal across species (e.g., Brunsting 1982).
2. Speed: The speed of an individual depended on body mass and body temperature (Morgan 1985, Hurlbert et al. 2008) and was calculated by applying the empirical relationship presented by Hurlbert et al. (2008).
3. Displacement: The displacement of an individual per time step depended on the speed of the individual and the directional persistence of movement during the particular time step.
4. Turning angle: The direction of movement of an individual was correlated across successive time steps, simulating a correlated random walk (Codling et al. 2008).
5. New position: The new position at the end of a time step was calculated from the previous position, the displacement, and the movement direction.

Table 1. State variables of simulated individuals.

| Variable name | Description | Possible values | Units |
|---|---|---|---|
| Body mass | Fixed species-specific body mass of species 1–10 | 1, 2, 4, 7, 13, 25, 48, 91, 173, 330† | mg |
| Body temperature | Fixed body temperature across the simulation | 288, 291, 294, 297, 300, 303 (~15–30) | Kelvin (°C) |
| Position | *x*:*y* coordinate of the grid cell in the area | 1–2000:1–2000 | . . . |
| Previous direction | Direction of movement in the previous time step | 0–360 | degree |
| New direction | Direction of movement in the current time step | 0–360 | degree |
| Mortality status | Individual is alive or dead following a trapping event | Alive, dead | . . . |
| Activity | Whether an individual is active and moves | Yes, no | . . . |
| Start activity period | First time step of activity period; assumed to equal across individuals | 3601 | time step per day |
| End activity period | First time step where the individual is inactive following an activity period; assumed to equal across individuals | 6481 | time step per day |

† Values are logarithmically spaced covering a proper subset of the body mass range of ground-dwelling arthropod species sampled in two Central European grasslands (Table S1 in Rzanny and Voigt 2012, Gossner et al. 2015); species smaller than 1 mg (≤3 mm body length) were not covered in our study.

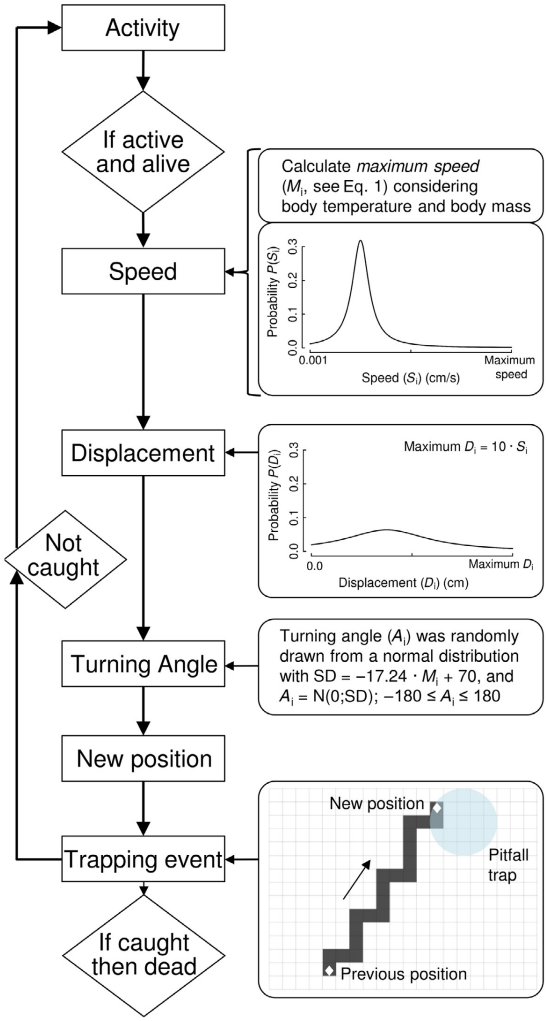


Fig. 1. Overview of model processes during one model time step. The processes "speed" and "displacement" use a truncated Cauchy probability distribution. The shown Cauchy distributions represent actual distributions used in the model (see Appendix S1 for empirical parameterization).

6. Trapping event: An individual died and was added to the number of sampled individuals if it was caught in a pitfall trap during the movement from the previous to the new position.

*Design concepts.—*

1. Basic principles: Animal movement is a continuous process of changes in speed and direction that is generally discretized to a sequences of steps in order to facilitate model simulations (Pyke 2015). The movement of ground arthropods at the scale of multiple body lengths has been identified as correlated random walk; that is, the movement direction at a time step depends on the direction at the previous step (directional persistence; Kareiva and Shigesada 1983, Bovet and Benhamou 1988, Wallin and Ekbom 1988, Codling et al. 2008, Pyke 2015). The specific assumption about the degree of directional persistence influences the simulated movement pattern of ground arthropods and, thus, affects the probability of a "trapping event" and the sampling bias, which concerns the purpose of our study (see empirical model parameterization in Appendix S1).
2. Emergence: A trapping event, and thus the number of sampled individuals, emerged purely from the movement of ground arthropod individuals across the simulated area with pitfall traps integrated. To limit side-effects of the specific position of each individual at simulation start, each simulation experiment with a particular parameter set was repeated 50 times and results were averaged for model analysis.
3. Interaction: No interactions were considered among ground arthropod individuals or between ground arthropod individuals and pitfall traps, such as repelling or attraction due to preservative type in the trap (simplifying findings from Knapp and Ruzicka 2012 and Brown and Matthews 2016).
4. Stochasticity: Some key processes of ground arthropod movement were modeled by assuming they are random and follow a certain probability distribution including speed, displacement, and turning angle (see probability distributions within Fig. 1). Considering probability in model simulations was important to reflect differences in the specific movement path across individuals of one species.
5. Observation: During simulation experiments, individual and species-level factors were observed. This includes the trapping events across individuals and the proportion of sampled individuals per species.

*Input data.*—The model does not use time-varying inputs, that is, input data representing time-varying processes in the model (Grimm et al. 2010).

*Initialization.*—At the start of each simulation experiment, each individual was placed at a random cell of the 400-$m^2$ simulated area, where $x$ and $y$ coordinates of the cell were each randomly chosen from a uniform distribution. In case an individual was placed at a cell defined as pitfall trap, new $x$ and $y$ coordinates were drawn. The initial movement direction of each individual was randomly chosen from a uniform distribution between 0 and 359, where 0 would create movement along the $y$-axis with a constant $x$ coordinate value. The body mass and body temperature of each individual were set at the start of a simulation experiment. Pitfall traps were installed across the whole simulation experiment at a position specific to one of the six trap arrangements as shown in Appendix S3: Fig. S1.

*Submodels.*—

1. Activity: At the first time step of each full hour, it was checked across all individuals that are alive whether the activity period starts or finishes, applying the values of the state variables "start activity period" and "end activity period" (Table 1). The activity status of an individual may changed or not changed accordingly. During the activity period, resting behavior and intermittent movement were excluded; that is, speed was always larger than zero (simplifying findings of Firle et al. 1998 and Reynolds et al. 2015). An individual could be active only if it is alive (see process "trapping event").
2. Speed: The speed of a ground arthropod individual depends mostly on the body mass, the body temperature, and the behavioral mode (Morgan 1985, Hurlbert et al. 2008, Benhamou 2014). In our model, the actual speed $S_i$ (cm/s) of an individual $i$ per time step was derived by a two-step process.

   First, the potential maximum speed $M_i$ (cm/s) of the individual $i$ was calculated considering both body temperature $t_i$ (Kelvin) and body mass $m_i$ (g) (Hurlbert et al. 2008):

$$M_i = 4.3 \times 10^{11} \times (m_i^{0.25}) \times e^{\left(\frac{-E}{k \times t_i}\right)} \quad (1)$$

   where a general temperature effect on biological rates based on reaction kinetics is described by a Boltzmann factor $e^{(-E/kT)}$, with $T$ being the temperature in Kelvin, $E$ the average activation energy of reactions involved in metabolism ($E$ = 0.65 eV), and $k$ the Boltzmann's constant ($8.62 \times 10^{-5}$ eV·$K^{-1}$; Gillooly et al. 2001). This model provides an accurate relationship between metabolic rate and temperature over the range of most biological activity (0–40°C).

   Second, $S_i$ was drawn randomly from a Cauchy distribution ranging from 0.001 to $M_i$. To ensure a constant shape of the Cauchy distribution across different $M_i$, the Cauchy distribution was truncated to the range from 0.001 to 20 yielding a random value $S_{i,20}$. The actual speed $S_i$ was subsequently scaled to have the maximum $M_i$ by $S_i = S_{i,20}/20 \times M_i$.
   The Cauchy distribution is characterized by a "fat tail" yielding a low number of high-speed values but a high number of low-speed values, which relates to empirical proportions of the movement and the search behavioral mode of animals in general (Benhamou 2004, 2014). The specific shape of the Cauchy distribution is defined by the two parameters scale ($\gamma$) and location ($x_0$; see Appendix S1 for empirical parameterization).
3. Displacement: The air-line displacement $D_i$ of an individual $i$ during one time step (10 s) does depend on both the speed $S_i$ (cm/s) and the degree of directional persistence during this time step. The displacement $D_i$ was drawn randomly from a Cauchy distribution truncated to the range from 0 to $10 \times S_i$. This can result in rare events of either no displacement ($D_i = 0$) or moving straight ($D_i = S_i \times 10$). Similar to the calculation of $S_i$, an initial value $D_{i,20}$ was drawn from a Cauchy distribution truncated to 0–20, and then, $D_i$ was subsequently scaled to have the maximum $10 \times S_i$ by $D_i = D_{i,20}/20 \times 10 \times S_i$ (see Appendix S1 for empirical parameterization).

4. Turning angle: At the beginning of each time step, the movement direction of an individual $i$ during the previous time step may be changed by the turning angle $A_i$. The turning angle $A_i$ was randomly chosen from a normal distribution with a certain standard deviation (SD). Values outside −180 and 180 degree were rejected and new values drawn, effectively creating a wrapped normal distribution. The mean of the normal distribution was set to zero assuming an equal proportion of left and right turns. Individuals change the movement direction at scales related to their body length (Pyke 2015) and may increase directional persistence across time steps with increased speed. We calculated SD per individual $i$ from a linear equation with a negative slope:

$$\mathrm{SD}_i = a \times M_i + b \quad (2)$$

where $M_i$ is the maximum speed at the particular time step and $a$ and $b$ are constants (see Appendix S1 for empirical parameterization). $\mathrm{SD}_i$ decreases with increasing maximum speed $M_i$. Thus, increasing body mass and temperature results in an increasing directional persistence across modeled time steps.
The new direction of movement $A'_i$ (i.e., an absolute angle) was calculated by adding the turning angle $A_i$ to the previous direction of movement. To ensure $0 \leq A'_i \geq 360$ degree, 360 is either added to $A'_i$ if $A'_i < 0$ or subtracted from $A'_i$ if $A'_i > 360$.

5. New position: The new values for the $x$ and $y$ coordinates were calculated as follows:

$$X_{i,\mathrm{new}} = X_{i,\mathrm{prev}} + (D_i \times \cos A'_i) \quad (3a)$$

$$Y_{i,\mathrm{new}} = Y_{i,\mathrm{prev}} + (D_i \times \sin A'_i) \quad (3b)$$

where $A'_i$ was converted from degree to radian beforehand ($A'_{i,\mathrm{radian}} = A'_{i,\mathrm{degree}} \times \pi/180$). In case $X_{i,\mathrm{new}}$ or $Y_{i,\mathrm{new}}$ was lower than one or larger than 2000 (outside of the simulated area), the value 2000 was either added or subtracted. Positional $x$ and $y$ coordinates were rounded to integer values.

6. Trapping event: A trapping event occurred; namely, an individual was caught in a trap and died, if at least one cell of the movement path from the previous to the new position equals a cell of the simulated area designated as pitfall trap. The movement path during one time step was modeled explicitly, simplified to an almost straight path between the previous and the new position using Bresenham's line algorithm (Bresenham 1965). We represented a round pitfall trap by means of the quadratic cells assuming a certain catching probability per pitfall trap cell (Appendix S3: Fig. S2). The cell-specific catching probability equals the proportion of the cell covered by the pitfall trap. In case an individual moves at a cell that is defined as trap but covered by the trap <100%, the occurrence of a trapping event was drawn randomly from a uniform distribution between 0 and 100. The individual got caught if the random number drawn is lower than the proportion of the cell covered by the trap.

### *Simulation experiments*

We conducted 840 simulation experiments systematically varying pitfall trap number, pitfall trap arrangement, body temperature, and population density to assess the species-specific sampling bias. In each simulation experiment, the movement and sampling of individuals across all 10 species were modeled, covering body masses between 1 and 330 mg (Table 1).

Five different numbers of pitfall traps were simulated (1, 2, 4, 8, and 12). Simulation experiments with pitfall trap numbers 4, 8, and 12 covered four different spatial arrangements of pitfall traps (nested cross, two circle, transect, and grid; Appendix S3: Fig. S1). These four trap arrangements were either frequently used in field studies or subject of model simulation studies aiming to improve the reliability of pitfall trapping (Crist and Wiens 1995, Perner and Schueler 2004, Zhao et al. 2013, Chenchouni et al. 2015).

Ten different population densities were simulated (0.15, 0.2, 0.3, 0.4, 0.6, 0.8, 1, 2, 4, and 8 individuals/$m^2$). This range of population densities covers empirical data of arthropod taxa obtained by true density measurements, such as mark–release–recapture experiments, across arable land and grasslands (Lovei and Sunderland 1996, Thomas et al. 1998, Elliott et al. 2006). The selected population densities follow a logarithmic curve.

The particular body temperature across all individuals ranged from 15° to 30°C (Table 1). This range fits well the ambient temperatures in places such as Central Europe and northeast China throughout the vegetation period (Appendix S4: Fig. S1), assuming that the body temperature exceeds the ambient temperature by 8°C (see section State variables and scales). We modeled a constant temperature for each simulation experiment, simplifying variation between day and night as well as variation across the 14 d of sampling.

### *Animation of simulated arthropod movement*

In addition to the theoretical description of how the model simulates the movement of ground arthropod species, an animation is provided showing in top view the simulated movement of three species (see Video S1; details described in Appendix S6, with Appendix S6: Fig. S1 providing a screenshot of the animation).

### *Data analysis*

The data analysis covered (1) the simulated movement pattern across species and (2) the sampling bias. The latter consisted of two main parts: the species-specific sampling bias and correction factor, and the bias in community-level metrics. The R language version 3.2 together with the vegan package version 2.3-5 was used for data analysis (R Core Team 2015, Oksanen et al. 2016).

According to the virtual ecologist approach, we differentiate between "simulated," "sampled," "observed," and "estimated" values of certain parameters. "Simulated" corresponds to the model input parameters, "sampled" corresponds to the individuals that fell into a pitfall trap virtually (i.e., trapping event), "observed" corresponds to species-specific parameters that were directly derived from the number of sampled individuals, and "estimated" corresponds to community-level metrics derived from "observed" parameters. In a simulation experiment, for example, the "simulated" abundance of a species may be 400 and the number of "sampled" individuals 100, resulting in the "observed" sampling bias of 0.75 (species-specific proportion of simulated individuals *not* sampled). Subsequently, the RAD and the Shannon diversity could be "estimated" for a particular community of multiple species with certain "simulated" abundance and an "observed" sampling bias per member species.

*Movement pattern.*—We used extra model simulations without pitfall trapping to analyze the species-specific movement pattern across 10 species with 1–330 mg body mass at 24°C body temperature. Across 8 h of movement, we recorded four key elements of animal movement for 1000 simulated individuals per species: the movement speed, the turning angle, the displacement at each time step, and the air-line displacement after 8 h.

*Species-specific bias.*—For each of the simulation experiments, the number of sampled individuals was recorded per species and per day. For the data analysis, the averaged results of 50 repetitions per simulation experiment were used, essentially eliminating effects of the random start position of individuals. The information about the number of sampled individuals was used to calculate per simulation experiment the observed pitfall trap sampling bias after 14 d of simulated sampling.

Analyses covered individual and combined effects on the observed sampling bias from variation in pitfall trap arrangement, pitfall trap number, population density, and body temperature. Specifically, we analyzed (1) how the mean, the minimum, and the maximum sampling bias across species were affected by trap number and trap arrangement, each for three different body temperatures (15°C, the average across all body temperatures considered, and 30°C); (2) how the sampling bias of each species was affected by its median speed, considering each combination of trap number and trap arrangement separately; (3) how the sampling bias was affected by (i) body temperature, (ii) simulated population density, and (iii) body mass; (4) how species-specific correction factors, for deriving unbiased relative abundance, are related to species body mass.

The observed species-specific sampling bias of species $i$ was defined as:

$$B_i = 1 - \frac{n_i}{N_i} \tag{4}$$

where $N_i$ is the simulated abundance and $n_i$ is the sampled abundance of the species $i$. Accordingly, the simulated abundance of species $i$ (the unbiased *absolute* abundance in the field) can be

calculated from the sampling bias and the sampled abundance of this species:

$$N_i = \frac{n_i}{(1 - B_i)} \quad (5)$$

We defined the species-specific correction factors for deriving unbiased *relative* species abundance as proportional to the inverse of the proportion of caught individuals:

$$\delta_i \sim \frac{N_i}{n_i} = \frac{1}{1 - B_i} \quad (6)$$

where $i$ is the species index, $\delta$ is the correction factor, and $B$ is the observed sampling bias (Eq. 4). Multiplying the sampled abundance $n_i$ of species $i$ by the correction factor $\delta_i$ gives the unbiased *relative* species abundance $N_{R,i}$ (i.e., relative to the simulated number of individuals or the unbiased absolute abundance in the field):

$$N_{R,i} = n_i \times \delta_i \quad (7)$$

We analyzed the relationship between the correction factor $\delta$ and species body mass $m$, which has a high relevance in community ecology and can be easily estimated for each species. This relationship we assumed to be of the form:

$$\delta_i \sim m_i^{\beta} \quad (8)$$

where $\beta$ is the strength of the body mass effect on the correction factor, or rather the slope of the relation between correction factors and body mass.

*Community-level bias.*—Communities were not simulated in extra simulation experiments. Species-specific values of simulated and sampled abundance from the above-described simulation experiments were used to create virtual communities and calculate community-level metrics. Communities were assembled from 10 differently sized species with 1–330 mg body mass (Table 1) and characterized by a specific RAD. In a community, the simulated population densities of the 10 member species followed a log curve. Species at ranks from 1 to 4 (with 3200, 1600, 800, and 400 individuals) were defined as *dominant* because their population abundance is larger than 10% of the most abundant species (sensu Grime 1998). We refer to the remaining species at ranks 5–10 as *subordinate* species. 50,000 random communities of ground arthropods were created by arranging the 10 species into different sequences along the abundance ranks. Of these communities, 378 were selected for analysis, using the ones with a realistic relationship between body mass and population abundance, that is, small species having a higher rank than larger species (for details, see Appendix S6). Additionally, we created two communities where the body mass across the abundance ranks strictly increases or decreases.

We calculated for all combinations of trap number and trap arrangement, averaged across all simulated body temperatures: (1) the simulated and the estimated relative abundance per species, displaying the RAD for the two "strict" communities and the average of the 378 random communities.

Further, we calculated for only the 378 random communities the following metrics across the combinations of all trap numbers, all trap arrangements, and three body temperatures (15°C, the average across all body temperatures considered, and 30°C): (2) the deviation of the estimated from the simulated species-specific abundance rank, (3) the proportion of simulated dominant species that were classified as subordinate species based on the estimated abundance ranks, and (4) the estimated and simulated Shannon diversity and Fisher's alpha.

## Results

### *Body mass-related movement pattern*

The relation between maximum speed and body mass was central to our simulations of pitfall trapping ground arthropod species (Eq. 1). Appendix S7: Fig. S1 presents the variation in four key elements of animal movement across the body masses used in our simulations. The median movement speed per time step increased with body mass from 0.2 for small species to 0.85 cm/s for large species. The median turning angle decreased from 37.9 to 8.4 degree. The median displacement during one time step and one day increased from 0.77 to 3.24 cm and 0.83 to 15.84 m, respectively. The simulated ground arthropod movement included rare events of extreme values in speed, displacement, and turning angle across all species, meeting an essential property of animal movement in general.

### Species-specific sampling bias

*Trap number and arrangement.*—Our model simulations highlight a strong decrease in the sampling bias with increasing pitfall trap number, consistently across trap arrangements (Fig. 2). When increasing the trap number from 1 to 2, 4, 8, and 12, the sampling bias decreased from 0.94 to 0.89, 0.82, 0.71, and 0.62 averaged across all species, temperatures, trap arrangements, and population densities (Fig. 2B). Importantly, the difference in the sampling bias between small and large-sized species increased with increasing pitfall trap number from 0.13 to 0.23, 0.36, 0.52, and 0.60, respectively. Consequently, the increase in trap numbers strongly affected two important metrics at the same time: lowering the mean sampling bias and increasing the variation in the sampling bias between small and large species.

We found considerable differences across the four trap arrangements nested cross, two circle, transect, and grid only when applying eight or 12 pitfall traps (Fig. 2; Appendix S6; animation in Video S2). Notably, eight traps arranged as grid or two circle produced about the same average sampling bias as 12 traps arranged as nested cross or diagonal transect. Body temperature had a strong impact on the absolute values of the sampling bias, but not on the relative differences in the sampling bias across pitfall trap number and arrangement.

*Movement speed.*—Our simulation experiments reveal a non-linear relationship between the sampling bias of a species and its median movement speed (Fig. 3). The shape of this relationship was considerably affected by the number of pitfall traps, but not so much by the specific trap arrangement. The sampling bias of very slow-moving species was high across all pitfall trap numbers. The sampling bias of fast-moving species varied strongly with changes in trap number.

*Temperature, population density, and body mass.*—The sampling bias decreased non-linearly with an increasing body temperature (Appendix S8: Fig. S1). With an increasing number of pitfall traps, the effect of body temperature on the sampling bias increased. A rise in body temperature from 15° to 30°C decreased the average sampling bias across species by about 0.1 if one trap was used and 0.5 if 12 traps were used (Appendix S8: Fig. S1).

Surprisingly, an increase in population density from 0.15 to 8 individuals per $m^2$ had no effect on the sampling bias (Appendix S8: Fig. S2). Clearly, the absolute number of sampled individuals increased with increasing population density but the proportion of simulated individuals that were sampled remained unaffected. This can be explained as a consequence of the random distribution of the individuals at the start of each simulation experiment, which ensures a certain species-specific probability for an individual to become sampled during the simulation experiment. This probability may equal "1 minus the species-specific sampling bias" and did not depend on population density because interactions between individuals were not considered.

The body mass of a species had a non-linear negative impact on the sampling bias (Appendix S8: Fig. S3, log–log scaled). The sampling bias was non-linearly related to body mass due to the non-linear effects of body mass on maximum speed adding to the non-linear effects speed on sampling bias (Eq. 1 and Fig. 3).

*Correction factor.*—The correction factors were linearly related to species body mass on a log–log scale (Fig. 4A; see Appendix S9: Fig. S1 for temperature effects). The fitted linear models had very high $R^2$ values around 0.99. The slopes varied significantly between trap numbers and temperatures (Fig. 4B; Appendix S9: Fig. S2). Slopes were steeper and more negative with lower numbers of pitfall traps and temperatures indicating larger differences in the sampling bias and the correction factor between small and large species. For example, the slope was −0.44 for eight and −0.49 for four pitfall traps arranged as nested cross. Realistic estimates of unbiased relative species abundance can be obtained by applying the slope (β) to Eq. 8 and the resulting species-specific correction factor (δ) to Eq. 7.

Assuming eight traps arranged as nested cross, for example, the correction factor would be 0.105 for a species of 100 mg ($100^{-0.49}$) and 0.712 for a species of 2 mg ($2^{-0.49}$) yielding unbiased *relative* species abundance when applied to Eq. 7. The nested cross arrangement of pitfall traps may be particularly useful for estimations of unbiased relative species abundance because of the small 95% confidence interval of the slope, implying that the relation between the correction factor

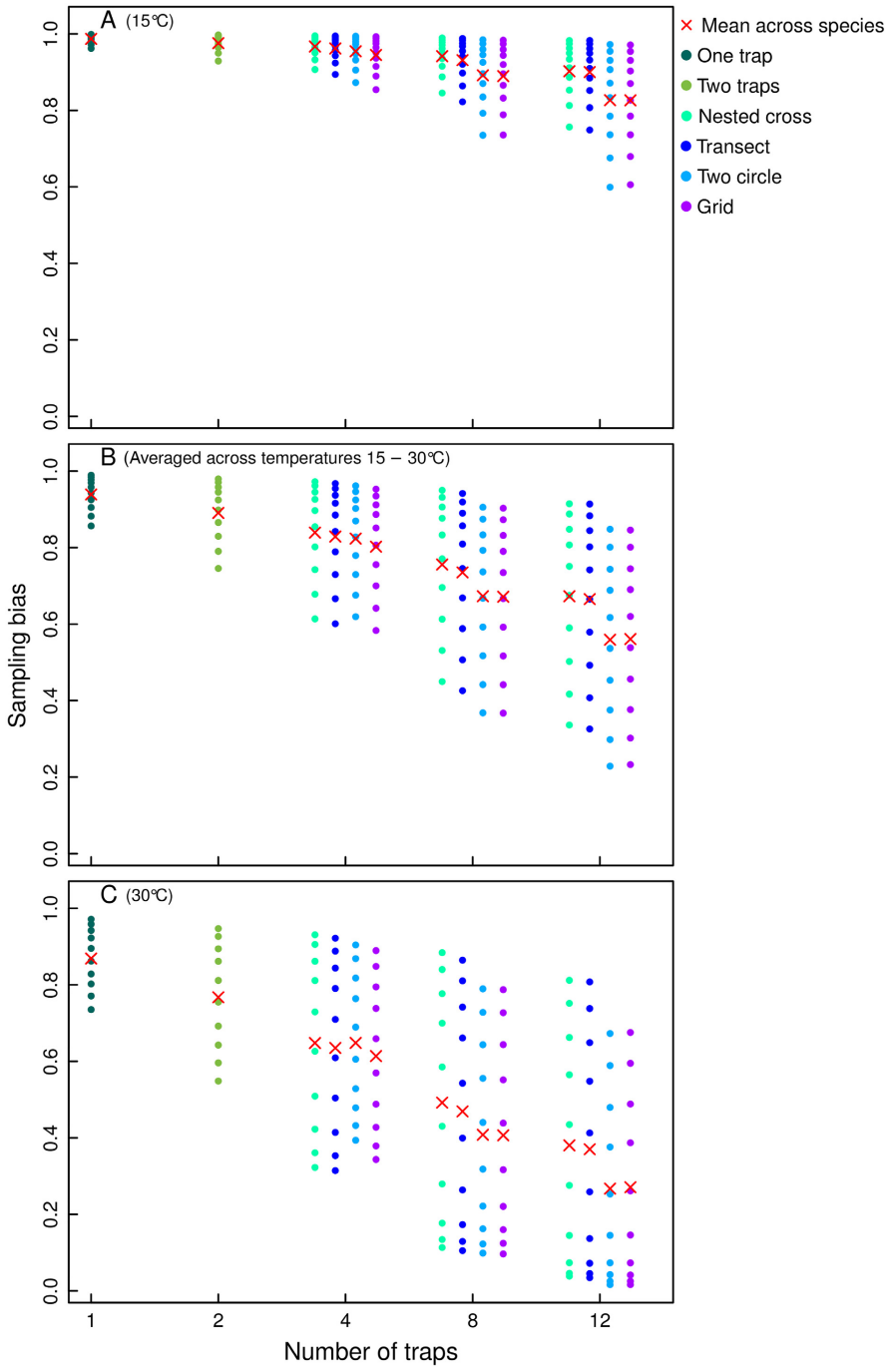


Fig. 2. Species-specific sampling bias, that is, the proportion of simulated individuals not sampled, per pitfall trap number and trap arrangement (Appendix S3: Fig. S1) after simulated pitfall trap sampling of 14 d, with 8 h of activity per day. Values for 10 different species (1–330 mg body mass) and the mean across these species are shown. Values are averaged across simulation experiments with 10 different population densities. The pitfall trap arrangement is color-coded (see legend). The minimum and maximum values of the sampling bias per trap

(*Fig. 2. Continued*)
number and arrangement correspond with the largest and smallest species, respectively. Panels show results for (A) 15°C body temperature, (B) averages across six different body temperatures spanning 15–30°C, and (C) 30°C body temperature.

and the body mass is more linear than for other trap arrangements. Note that the correction factor derived from Eq. 8 is proportional to the sampling bias (see Eq. 6).

### *Community-level effects of the sampling bias*

*Rank-abundance distribution.*—The estimated RAD generally differed from the simulated RAD across pitfall trap numbers and trap arrangements (Fig. 5). Differences between the simulated and estimated RAD were mainly driven by the body mass–dominance relationship. The estimated RAD was flatter than the simulated RAD for arthropod communities with reasonable species abundance ranks, structured in the way that large species were rare and small species abundant (Fig. 5B, C; Appendix S5: Fig. S1). Larger, rarer species are relatively over-represented in pitfall trap catches from such arthropod communities, thus inflating diversity estimates using Shannon diversity and Fisher's alpha (Appendix S10). The opposite pattern, that is, the estimated RAD was steeper than the simulated RAD, was found when large species were abundant and small species rare (Fig. 5A). Further, the difference between the estimated RAD and the simulated RAD decreased with increasing trap numbers (Fig. 5).

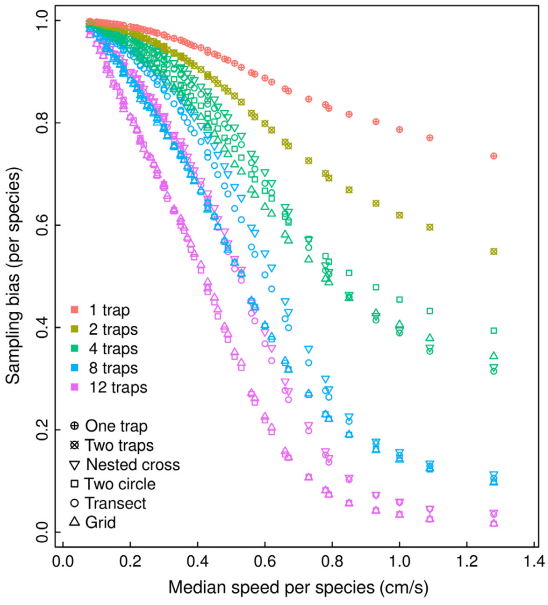


Fig. 3. The relationship between the species-specific sampling bias and the median speed of the species, shown for different combinations of pitfall trap number (color-coded) and trap arrangement (symbols; applicable for 4–12 traps). Speed values are averaged across individuals per species and cover six different body temperatures (Table 1).

*Species-specific abundance rank.*—Pitfall trap sampling can produce a bias in the estimated abundance rank of a species (Fig. 6). We find that generally the estimated rank of small species is higher than the simulated rank, while the estimated rank of large species is lower than the simulated rank (notes: Low rank means dominance; in Fig. 5, a low rank is consistent with a lower number at the *x*-axis with the highest-abundant species at rank 1). The difference between the estimated and the simulated abundance rank decreased with increasing pitfall trap number and body temperature.

*Classification of dominant species as subordinate.*—Our model simulations revealed that an average proportion of about 25% of the simulated dominant species were classified as subordinate species by pitfall trap sampling due to the bias in estimated abundance ranks (Fig. 7B). In return, this means that an equal number of simulated subordinate species was estimated as dominant species. On average, across 378 random communities (Appendix S5), this finding remains valid for changes in pitfall trap number, trap arrangement, and body temperature (see median [orange bars] and average [red dots] of communities in Fig. 7). For low body temperatures and low pitfall trap numbers in particular, the proportion of simulated dominant species that are detected as subordinate strongly varied between zero and 75%, thus depending mainly on the community structure in terms of the body mass distribution across the abundance ranks. The effect of community structure, however,

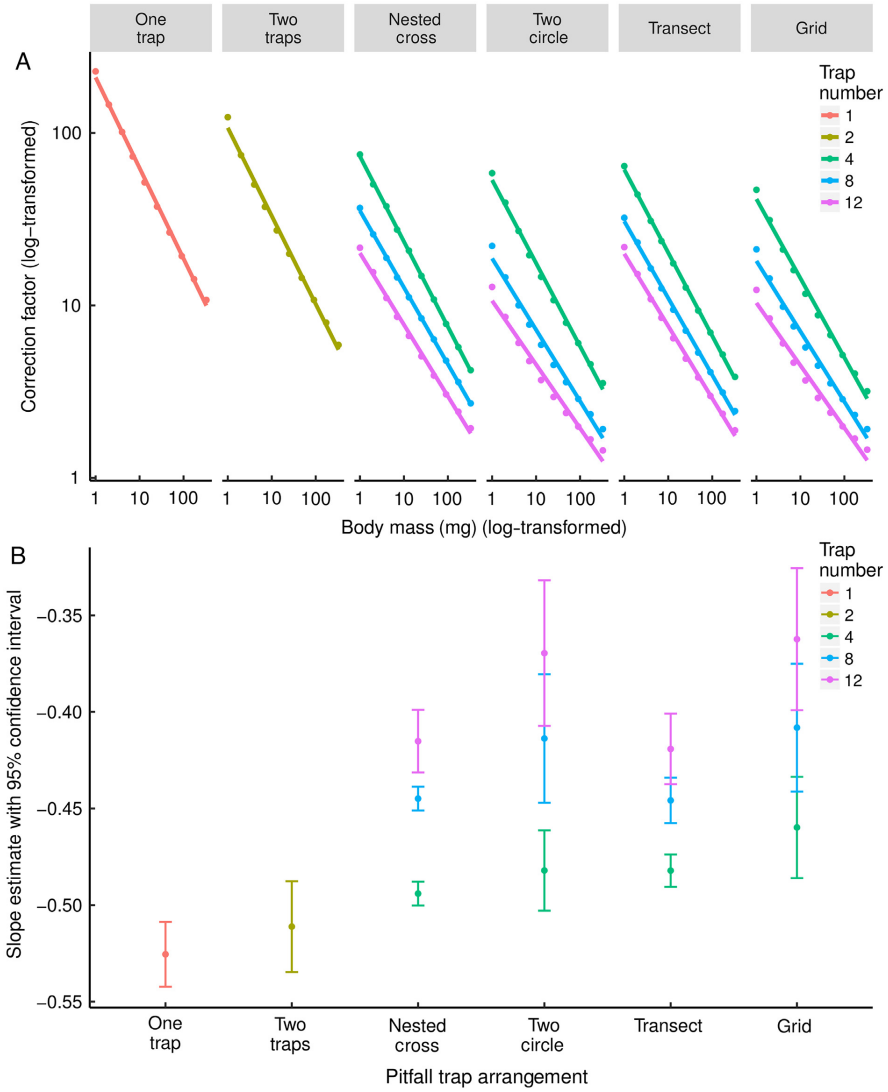


Fig. 4. (A) The relationship between body mass and the correction factor for deriving unbiased relative species abundance per trap number and trap arrangement (Appendix S3: Fig. S1), averaged across six different body temperatures (15–30°C; see also Appendix S9: Fig. S1). The individual values per species (dots) and the linear regression line are shown. (B) The slope of the regression lines from panel A is shown together with the 95% confidence interval.

generally diminished with increasing numbers of pitfall traps.

## Discussion

Our study clearly shows that the pitfall trap sampling bias strongly decreases with increasing body mass, body temperature, and trap number, while the spatial arrangement of pitfall traps has only limited effects (Fig. 2). The population density does not affect the sampling bias; hence, a specific parameterization of bias correction across different studies or study years is acceptable even if the densities of sampled species vary strongly. We derived species-specific correction factors that allow unbiased estimates of relative

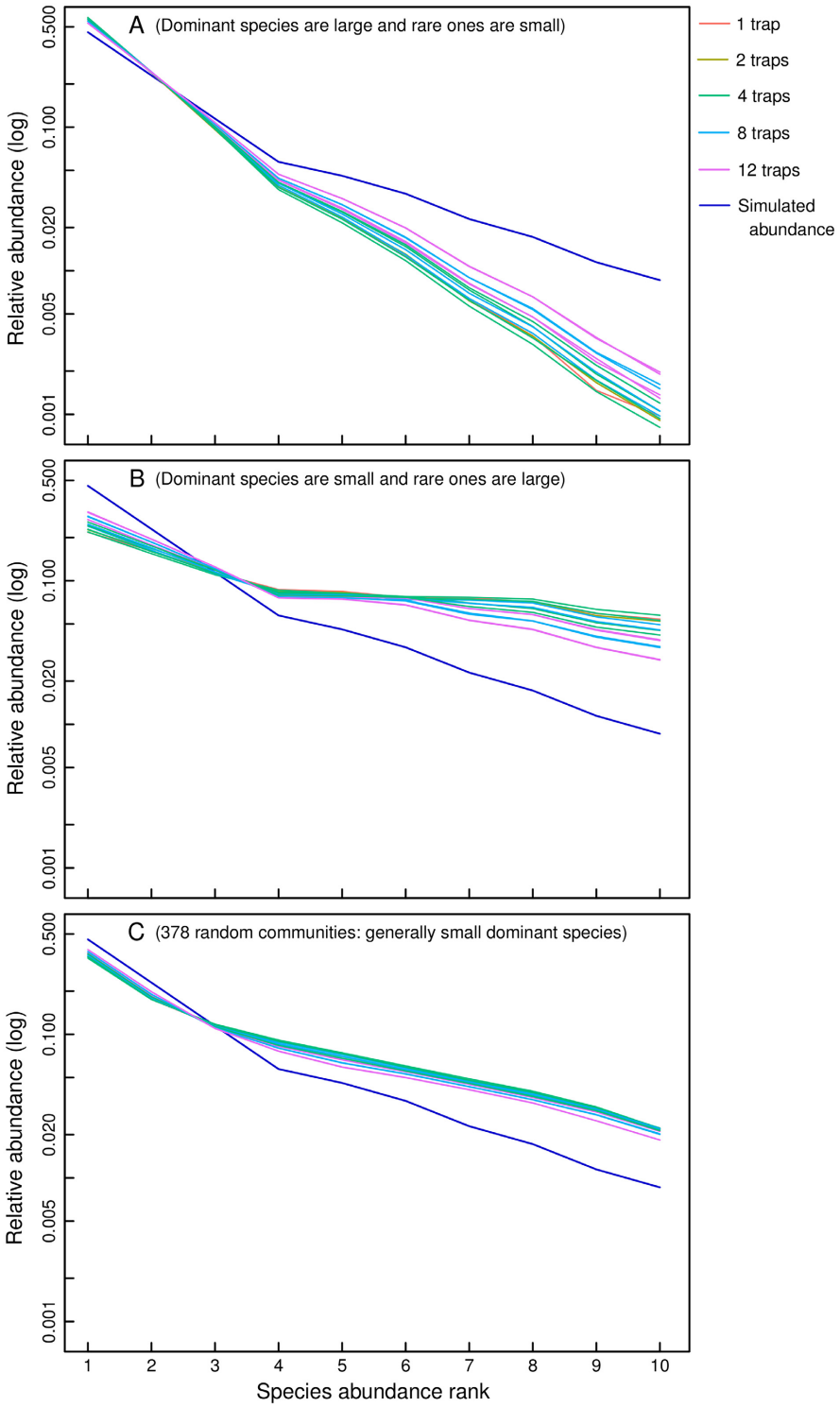


Fig. 5. The rank-abundance distribution (RAD) of the simulated population abundance (dark blue; logarithmically spaced from 8 to 0.15 individuals/m$^2$) and the observed population abundance (see legend for colors). The

(*Fig. 5. Continued*)
RAD from observed abundance is shown for each of the 14 different combinations of pitfall trap number and trap arrangement, but only differences in trap number are color-coded. The *y*-axis shows relative abundance per species and the *x*-axis the abundance rank where species with rank 1 is the species with highest relative abundance. Panels show different community structures, that is, different sequences of species body mass across abundance ranks: (A) Body mass decreases with increasing simulated abundance rank—the largest species is most abundant (rank 1); (B) body mass increases with increasing simulated abundance rank—the smallest species is most abundant; and (C) average of 378 random communities, which are characterized by a reasonable body mass–abundance relationship (smaller species having generally a higher rank than larger species, Appendix S5).

species abundance to be derived knowing only species body mass (Fig. 4). Interestingly, our analyses reveal that the variation in the sampling bias between differently sized species scales up to a bias in community metrics that is clearly indicated by a less steep RAD, which results in an overestimation of community diversity and incorrect identification of species dominance (Figs. 5, 7). We presented an allometric individual-based model that can simulate the movement and pitfall trap sampling of multiple, actively hunting ground arthropod species across the range of body masses from 1 to 330 mg.

### *The species-level bias*

Our model simulations highlight considerable changes in the movement of ground arthropods with increasing body mass. Large species move at higher speeds and change their direction of movement less often than small species do. Hence, with increasing body mass, species displace more and may be considered more active. This is consistent with the commonly known biases of activity density measures in pitfall trap sampling toward larger, faster species (Mommertz et al. 1996, Lang 2000).

Our study reveals that the spatial arrangement of pitfall traps has only limited effects on the sampling bias (Figs. 2, 3). This is an unexpected result considering the effort of previous studies in finding an optimized trap arrangement to provide reliable pitfall trap samples (Crist and Wiens 1995, Perner and Schueler 2004, Zhao et al. 2013). Yet, we find that the sampling bias is clearly lower for the two-circle arrangement than for the nested cross, which is consistent with theoretically and empirically derived findings of Zhao et al. (2013).

The number of pitfall traps strongly impacts the sampling bias. This effect varies across species revealing a trade of concerning the optimal number of pitfall traps: The mean sampling bias decreased when the number of traps increased but at the same time the differences in sampling bias between small and large species strongly increased (Fig. 2). Thus, a higher number of pitfall traps mainly reduces the sampling bias of large species and increases the importance of correcting the species-specific sampling bias. Overall, we recommend either the grid or two-circle arrangement of 4–8 traps per 400 $m^2$ to both moderate the drawbacks of a high pitfall trap number and yield a low average sampling bias.

Environmental conditions in general and the ambient temperature in particular are important factors that constrain arthropod movement and thus affect the pitfall trap sampling bias (Melbourne 1999, Hurlbert et al. 2008, Wang et al. 2014). This is because the body temperature of ground arthropods is correlated with the ambient temperature (Casey 1976, Morgan 1985). We find accordingly that the sampling bias strongly decreases with increasing body temperature (Appendix S8: Fig. S1). Our findings are consistent with field experiments and a statistical correlation approach showing that the number of sampled individuals increases with mean daily temperature (Brunsting 1981, Thomas et al. 1998, Saska et al. 2013, Wang et al. 2014).

The species-specific sampling bias is strongly related to the movement speed and the number of pitfall traps (Fig. 3). Knowledge of this bias could be used to estimate unbiased absolute species densities in the field. The movement speed of ground arthropod species can either be measured by observations directly in the field or estimated from body mass and body temperature. Body mass of species sampled in field studies can be measured or derived from the literature. Body temperature can be estimated if the ambient temperature is measured frequently (e.g.,

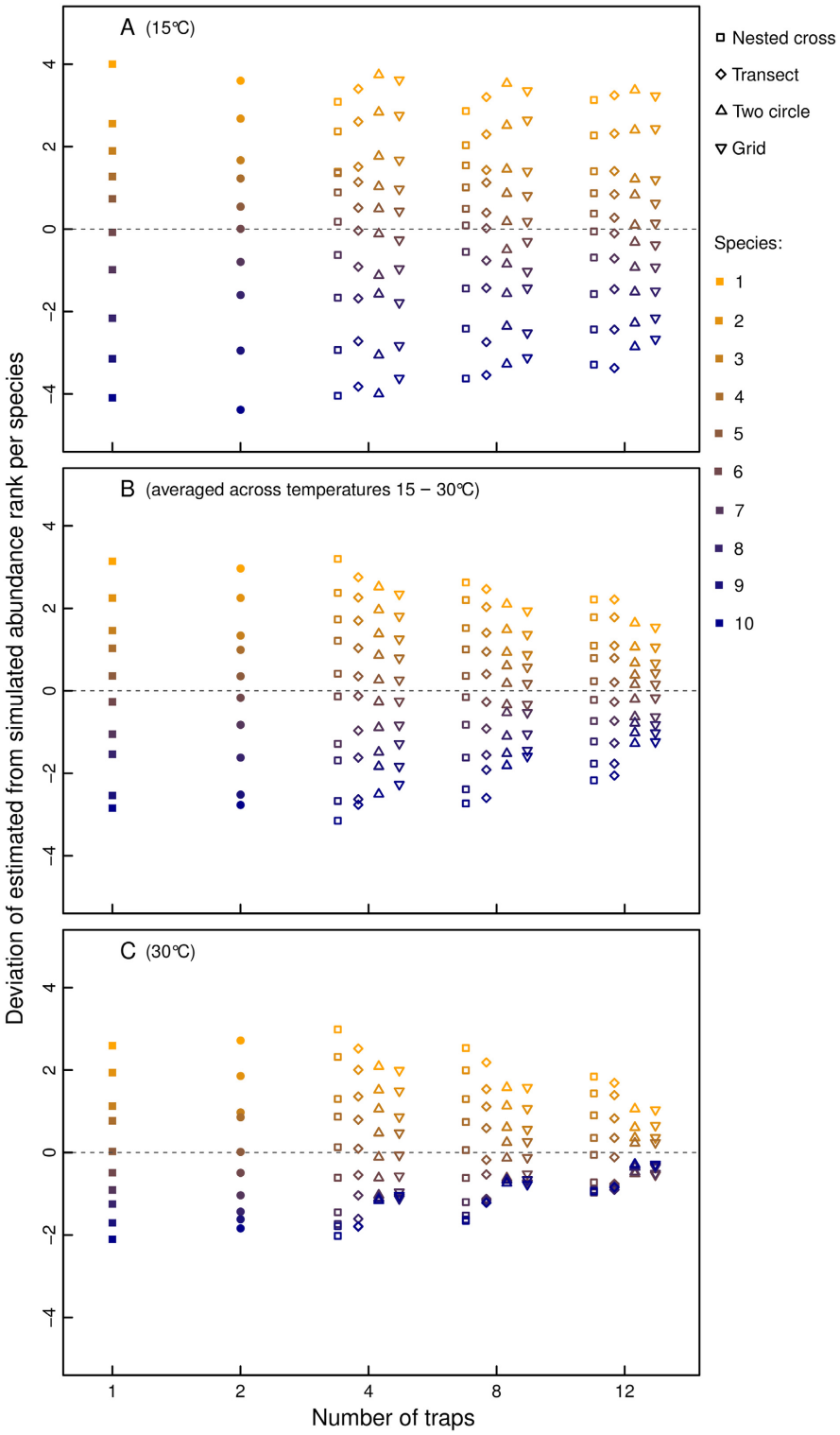


Fig. 6. Difference between simulated and estimated abundance rank per species, shown for different

(*Fig. 6. Continued*)
combinations of pitfall trap number and trap arrangement (full colored symbols for "one trap" and "two traps" arrangements; see legend for open symbols). Species are color-coded (orange: species 1 with 1 mg body mass, dark blue: species 10 with 330 mg body mass). A positive value means: The estimated abundance rank from pitfall trap sampling is higher than the simulated rank; that is, the estimated relative abundance is lower than the simulated one. A negative value means the inverse, and zero means no difference between simulated and estimated ranks. Values are averaged across 378 random communities (Appendix S5). Panels show results for (A) 15°C body temperature, (B) averages across six different body temperatures spanning 15–30°C, and (C) 30°C body temperature.

hourly) and knowledge on species' activity periods is available. For arthropod species with known activity periods, we propose using the species-specific median movement speed as simplifying proxy for estimating the sampling bias across trap numbers, because the movement speed in the field integrates many other factors that shape the sampling bias (Fig. 3). Further works are needed to test the practicability of this approach in field studies and the extent to which the sampling bias can be determined or reduced when compared to population densities estimated from, for example, quadrat sampling (Topping and Sunderland 1992, Spence and Niemelä 1994). For species with unknown activity periods, we suggest using body mass to calculate unbiased relative densities.

Relative species abundance is of prime importance for community ecology research being the basis for metrics such as the RAD. Our study reveals that a species-specific correction factor can be derived from species body mass alone, providing reasonable estimates of unbiased relative species abundance (similar to Hancock and Legg 2012). This correction factor offers a simple method to adjust pitfall trap data, as body mass could be easily measured for the species sampled and the sampling bias does not depend on population density (Appendix S8: Fig. S2; contrary to Perner and Schueler 2004). Bias correction would work across plots and studies along environmental and land-use gradients when taking into account potential differences in temperature and trap number and how these may affect the correction factor (Appendix S9: Fig. S2). Thus, there is potential to improve real-world data from previous and future sampling campaigns enabling much more reliable understanding of the impacts of climate and land-use change on community biodiversity.

### *The community-level bias*

Our study provides one of the first attempts to quantify the impact of the species-specific sampling bias on the community-level metrics: RAD, the dominance of species, and the species diversity, that is, Fisher's alpha and Shannon diversity.

The RAD of species is one of the most commonly analyzed patterns in ecology, generally showing a few dominant species and many less abundant or rare species in a community (McGill et al. 2007, Locey and White 2013). Our model results clearly show that the estimated RAD, based on observed species abundance from pitfall trap sampling, can strongly differ from the simulated RAD or rather the true RAD of the study community (Fig. 5). We find that the simulated distribution of species body masses across the abundance ranks essentially determines whether the estimated RAD is either more or less steep than the simulated, unbiased RAD. Generally, our results imply that a RAD estimated from pitfall trap sampling campaigns may be less steep than the real RAD (see Fig. 5B, C), because dominant species are commonly small, resulting in a high sampling bias, where the less abundant species are rather large, resulting in a comparably low bias (Siemann et al. 1999, Gossner et al. 2015). Any factor that increases the difference in the sampling bias between species may further increase the bias in the estimated RAD, such as elevating temperatures, higher trap numbers, and a larger range of body masses. The body masses we considered in our study range from 1 to 330 mg, which covers a subset of the body masses of arthropod species found by Gossner et al. (2015) in Central European grasslands. Hence, field studies that attempt to include all species occurring in a habitat may face an even larger bias in the estimated RAD as estimated from our simulations.

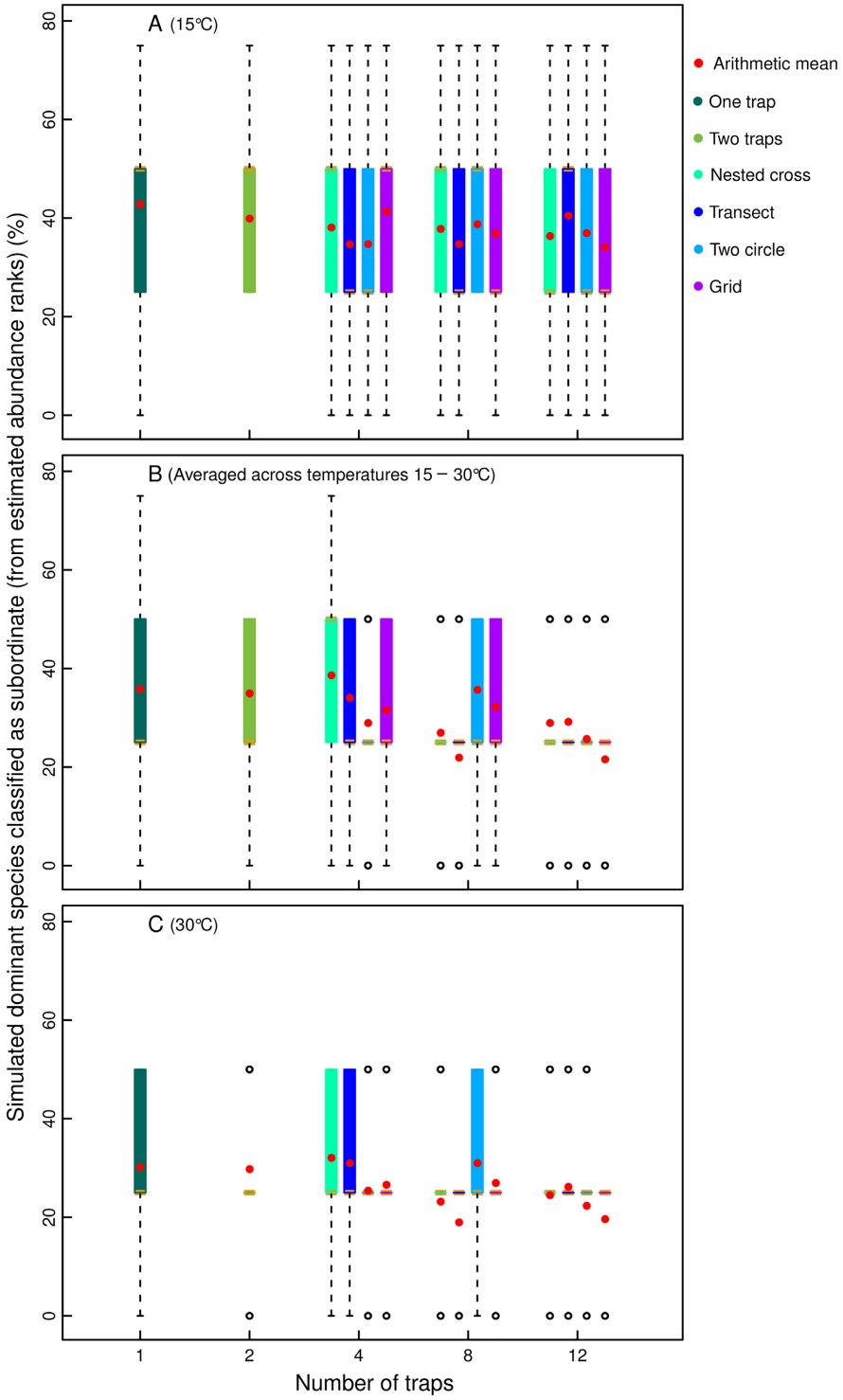


Fig. 7. Boxplot of the proportion of simulated dominant species that are classified as subordinate species based on estimated abundance ranks. The values are averaged across 378 random communities (Appendix S5). Values

(*Fig. 7. Continued*)
are shown for different combinations of pitfall trap number and trap arrangement (see legend for colors). Horizontal orange bars indicate the median, and the red dots show the arithmetic mean. The colored box ranges from the upper to the lower quartile, and the dotted whiskers cover the maximum and minimum values excluding outliers (black dots, if present). For some combinations of trap number and arrangement, the box and the whiskers match with the median. Species with one of the simulated abundance ranks 1–4 were defined as dominant species (see Methods section). Panels show results for (A) 15°C body temperature, (B) averages across six different body temperatures spanning 15–30°C, and (C) 30°C body temperature.

The RAD is clearly related to diversity indices that are important for both evaluating the condition of a community and estimating its vulnerability to environmental changes. Our results show that the estimated Shannon diversity and Fisher's alpha are generally larger than what we would expect from the simulated species abundance (Appendix S10: Figs. S1, S2). We argue that real Shannon diversity and Fisher's alpha values are generally lower than suggested from pitfall trap sampling campaigns; thus, population abundance within communities is less even and follows more the log series distribution than previously estimated. The Shannon diversity index, in particular, depends strongly on the body mass distributions across the abundance ranks, suggesting a high sensitivity to changes in the community structure. Importantly, this can jeopardize conclusions drawn from diversity analysis across communities differing in the species composition in general and the community structure in particular. Hence, the Shannon diversity of two communities can appear to be significantly different due to variations in body mass distributions. To avoid biased conclusions about differences between communities, field studies may need to apply species-specific correction factors of the sampling bias of pitfall trap data, or should test for differences in the body mass distributions.

In addition to the RAD of a community, the specific abundance rank is an important property of each single species enabling the assessment of the role it might play in ecosystem functioning. Dominant species are considered as particularly important for key ecosystem functions, while rare species may either work as insurance against future uncertainties or provide additional functions (Grime 1998, Mouillot et al. 2013). Our model simulations highlight that the estimated abundance rank of species can differ significantly from the simulated, unbiased abundance rank (Fig. 6). Generally, the relative population abundance is underestimated for small species and overestimated for large species by pitfall trap sampling. Empirical studies that analyze the arthropod community structure based on pitfall trap sampling may yield a bias in the functional importance of species underestimating small species and overestimating large species.

The classification of species into dominant and rare ones is an important tool in ecology to explore relationships between community diversity and functioning (Grime 1998). A difference between the estimated and the true abundance rank of species, however, can considerably impact the reliability of this classification. Our simulations reveal that a considerable proportion (about 25%) of the simulated dominant species are observed as subordinate (Fig. 7). Accordingly, an equal number of subordinate species is observed as dominant. This can constitute serious implications for the conclusions of studies on ecosystem function that focused on dominant species only. Furthermore, analysis of which species traits may drive key functions may need to be tested for reliability against variation in the set of species observed as dominant, for example, by statistically testing for effects of the body mass in general or its distribution across abundance ranks in particular.

In summary, pitfall trap sampling in field studies may generally produce flattened RAD yielding overestimations of community diversity and likely providing false results for the dominance classification of some species. Our findings extend the widely accepted species-specific bias in pitfall trap sampling campaigns to community-level metrics and urge caution to previous conclusions about the diversity and structure of ground arthropod communities when solely sampled with pitfall traps without bias correction.

*Model assumptions*

We deliberately used a simple model to simulate the movement and pitfall trap sampling of ground arthropods. Yet, we expand on previous simulation studies of pitfall trap sampling by considering parameter variation of multiple factors important for both ground arthropod movement and the design of a pitfall trap sampling campaign. In our simulations, we did not cover, however, other factors that were shown to influence the pitfall trap sampling bias of individual species, such as precipitation, litter depth, vegetation density, and the design of pitfall traps (Greenslade 1964, Spence and Niemelä 1994, Melbourne 1999, Lang 2000, Work et al. 2002, Koivula et al. 2003, Thomas et al. 2006, Cheli and Corley 2010, Brown and Matthews 2016). Though, our simplifying assumptions of a homogeneous, featureless landscape and plain traps are unlikely to affect the conclusions of our study as all simulation experiments were, in this respect, equal. Future simulation studies may particularly aim at integration of a plant diversity gradient facilitating sampling bias correction of multitrophic diversity studies in grassland (Rzanny and Voigt 2012), farmland (Klaus et al. 2013) and forest (Schuldt et al. 2015). Modeling the effects of vegetation structure and density on movement of ground arthropods should include plant individuals explicitly, so that the movement paths of ground arthropods result from a combination of external factors and the internal navigational capacity (Nathan et al. 2008).

*Implications*

The results of our individual-based model simulations help field studies to increase the reliability of species-specific data and any community-level metric estimated from pitfall trap sampling. The main factors that shape the species-specific sampling bias are body mass, temperature, and the number of pitfall traps (Fig. 2). Although the arrangement of traps is of minor importance when compared to trap number, the reliability of pitfall trap sampling can be increased by distributing traps uniformly within the sampling area. The bias in community-level metrics is linked to the species-specific biases and additionally shaped by the distribution of body masses across the abundance ranks (Fig. 5). To simplify the bias correction, studies should keep constant the trap number and trap arrangement across sampling sites and sampling periods whenever possible. Following the call of Brown and Matthews (2016) for standardized trap designs, we suggest to use either the nested cross or grid arrangement with standard trap numbers and spacing. For data analysis, species may be grouped into size classes assuming a similar bias for the species in one class and, thus, lowering the workload for bias correction across species. Species size classes may preferably cover logarithmically increasing ranges of body mass as body mass non-linearly affects the species-specific sampling bias (Appendix S8: Fig. S3).

Most research in community ecology derives diversity and community metrics based on species relative abundance, such as the RAD and species dominance within the community. One therefore may not need to correct observed species abundance on an absolute scale but rather on a proportional scale. Our analyses of the correction factor showed that species relative abundance can be re-set to unbiased values by species body mass when controlling for temperature variation, pitfall trap number and arrangement (Fig. 4B, Appendix S9: Fig. S2). For instance, a field study using two pitfall traps could correct relative abundance from species body mass with two scaling factors from the range between $-0.55$ and $-0.37$. The resulting interval in diversity and community metrics would be unbiased by pitfall trap sampling and could be used as a sensitivity test for conclusions drawn from individual studies or a meta-analysis across several studies.

We conclude that (1) the correction of the species-specific sampling bias to derive realistic absolute species abundance and (2) the use of body mass-related correction factors to derive true relative species abundance are a manageable task and necessary to reliably identify changes in species abundance and community diversity across time or habitats. Given that the species body masses are easily estimated for ground arthropods, the bias correction for true relative abundance should be a simple, practical approach for field studies to be widely adopted and tested. Also, the ambient temperatures (as proxy for body temperature) across the sampling periods are often available, facilitating estimations of the median movement speed and, subsequently, realistic indications of the sampling bias

and absolute densities per species (Fig. 3). Future studies may attempt to reanalyze available "activity density" data from previous pitfall trap sampling campaigns to advance our understanding of arthropod community structure both within certain habitats and along environmental gradients.

## Acknowledgments

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## Literature Cited

Benhamou, S. 2004. How to reliably estimate the tortuosity of an animal's path: Straightness, sinuosity, or fractal dimension? Journal of Theoretical Biology 229:209–220.

Benhamou, S. 2014. Of scales and stationarity in animal movements. Ecology Letters 17:261–272.

Bovet, P., and S. Benhamou. 1988. Spatial-analysis of animals movements using a correlated random-walk model. Journal of Theoretical Biology 131:419–433.

Bresenham, J. E. 1965. Algorithm for computer control of a digital plotter. IBM Systems Journal 4:25–30.

Brown, G. R., and I. M. Matthews. 2016. A review of extensive variation in the design of pitfall traps and a proposal for a standard pitfall trap design for monitoring ground-active arthropod biodiversity. Ecology and Evolution 6:3953–3964.

Brunsting, A. M. H. 1981. Distribution patterns, life-cycle and phenology of *Pterostichus oblongopunctatus* F (Col, Carabidae) and *Philonthus decorus* Grav (Col, Staphylinidae). Netherlands Journal of Zoology 31:418–452.

Brunsting, A. M. H. 1982. The locomotor activity of *Pterostichus oblongopuncta* Tus F. (Col., Carabidae). Netherlands Journal of Zoology 33:189–210.

Byers, J. A. 2001. Correlated random walk equations of animal dispersal resolved by simulation. Ecology 82:1680–1690.

Cardoso, P., et al. 2008. Rapid biodiversity assessment of spiders (Araneae) using semi-quantitative sampling: a case study in a Mediterranean forest. Insect Conservation and Diversity 1:71–84.

Casey, T. M. 1976. Activity patterns, body temperature and thermal ecology in two desert caterpillars (Lepidoptera: Sphingidae). Ecology 57:485–497.

Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecology Letters 14:922–932.

Cheli, G. H., and J. C. Corley. 2010. Efficient sampling of ground-dwelling arthropods using pitfall traps in arid steppes. Neotropical Entomology 39: 912–917.

Chenchouni, H., T. Menasria, S. Neffar, S. Chafaa, L. Bradai, R. Chaibi, M. N. Mekahlia, D. Bendjoudi, and A. S. Bachir. 2015. Spatiotemporal diversity, structure and trophic guilds of insect assemblages in a semi-arid Sabkha ecosystem. PeerJ 3:e860.

Codling, E. A., M. J. Plank, and S. Benhamou. 2008. Random walk models in biology. Journal of the Royal Society, Interface 5:813–834.

Collins, K. L., N. D. Boatman, A. Wilcox, and J. M. Holland. 2003. A 5-year comparison of overwintering polyphagous predator densities within a beetle bank and two conventional hedgebanks. Annals of Applied Biology 143:63–71.

Crist, T. O., and J. A. Wiens. 1995. Individual-movements and estimation of population-size in darkling beetles (Coleoptera, Tenebrionidae). Journal of Animal Ecology 64:733–746.

Diekötter, T., S. Wamser, V. Wolters, and K. Birkhofer. 2010. Landscape and management effects on structure and function of soil arthropod communities in winter wheat. Agriculture Ecosystems & Environment 137:108–112.

Elliott, N. C., F. L. Tao, K. L. Giles, S. D. Kindler, B. W. French, M. H. Greenstone, and K. A. Shufran. 2006. Ground beetle density in Oklahoma winter wheat fields. Southwestern Entomologist 31:121–128.

Ellis, M. V., and M. Bedward. 2014. A simulation study to quantify drift fence configuration and spacing effects when sampling mobile animals. Ecosphere 5:1–20.

Finke, D. L., and W. E. Snyder. 2010. Conserving the benefits of predator biodiversity. Biological Conservation 143:2260–2269.

Firle, S., R. Bommarco, B. Ekbom, and M. Natiello. 1998. The influence of movement and resting behavior on the range of three carabid beetles. Ecology 79:2113–2122.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science 293:2248–2251.

Gossner, M. M., N. K. Simons, R. Achtziger, T. Blick, W. H. O. Dorow, F. Dziock, F. Kohler, W. Rabitsch,

and W. W. Weisser. 2015. A summary of eight traits of Coleoptera, Hemiptera, Orthoptera and Araneae, occurring in grasslands in Germany. Scientific Data 2:150013.

Greenslade, P. J. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). Journal of Animal Ecology 33:301–310.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86:902–910.

Grimm, V., U. Berger, D. L. DeAngelis, J. G. Polhill, J. Giske, and S. F. Railsback. 2010. The ODD protocol: a review and first update. Ecological Modelling 221:2760–2768.

Halsall, N. B., and S. D. Wratten. 1988. The efficiency of pitfall trapping for polyphagous predatory Carabidae. Ecological Entomology 13:293–299.

Hancock, M. H., and C. J. Legg. 2012. Pitfall trapping bias and arthropod body mass. Insect Conservation and Diversity 5:312–318.

Hurlbert, A. H., F. Ballantyne, and S. Powell. 2008. Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants. Ecological Entomology 33:144–154.

Hutchison, M. A. S. 2007. Seasonality and life histories of two endemic New Zealand carabid beetles (Coleoptera: Carabidae): *Mecodema oconnori* Broun and *Megadromus capito* (White). New Zealand Journal of Zoology 34:79–89.

Iknayan, K. J., M. W. Tingley, B. J. Furnas, and S. R. Beissinger. 2014. Detecting diversity: emerging methods to estimate species diversity. Trends in Ecology & Evolution 29:97–106.

Kareiva, P. M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random-walk. Oecologia 56:234–238.

Klaus, V. H., et al. 2013. Does organic grassland farming benefit plant and arthropod diversity at the expense of yield and soil fertility? Agriculture, Ecosystems & Environment 177:1–9.

Klazenga, N., and H. H. Devries. 1994. Walking distances of five differently sized ground beetle species. M. J. Sommeijer and J. Van der Blom, editors. Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society (N.E.V.) 5:99–100.

Knapp, M., and J. Ruzicka. 2012. The effect of pitfall trap construction and preservative on catch size, species richness and species composition of ground beetles (Coleoptera: Carabidae). European Journal of Entomology 109:419–426.

Koivula, M., D. J. Kotze, L. Hiisivuori, and H. Rita. 2003. Pitfall trap efficiency: Do trap size, collecting fluid and vegetation structure matter? Entomologica Fennica 14:1–14.

Lang, A. 2000. The pitfalls of pitfalls: a comparison of pitfall trap catches and absolute density estimates of epigeal invertebrate predators in Arable Land. Anzeiger für Schädlingskunde = Journal of Pest Science 73:99–106.

Locey, K. J., and E. P. White. 2013. How species richness and total abundance constrain the distribution of abundance. Ecology Letters 16:1177–1185.

Lovei, G. L., and K. D. Sunderland. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annual Review of Entomology 41: 231–256.

McGill, B. J., et al. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters 10:995–1015.

Melbourne, B. A. 1999. Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. Australian Journal of Ecology 24:228–239.

Mommertz, S., C. Schauer, N. Kösters, A. Lang, and J. Filser. 1996. A comparison of D-Vac suction, fenced and unfenced pitfall trap sampling of epigeal arthropods in agroecosystems. Annales Zoologici Fennici 33:117–124.

Morgan, K. R. 1985. Body-temperature regulation and terrestrial activity in the ectothermic beetle *Cicindela tranquebarica*. Physiological Zoology 58:29–37.

Mouillot, D., et al. 2013. Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biology 11:e1001569.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the United States of America 105:19052–19059.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2016. vegan: community ecology package. https://cran.r-project.org/package=vegan

Parmenter, R. R., and J. A. MacMahon. 1989. Animal density estimation using a trapping web design: field validation experiments. Ecology 70:169–179.

Perner, J. 2003. Sample size and quality of indication—a case study using ground-dwelling arthropods as indicators in agricultural ecosystems. Agriculture, Ecosystems & Environment 98:125–132.

Perner, J., and S. Schueler. 2004. Estimating the density of ground-dwelling arthropods with pitfall traps using a nested-cross array. Journal of Animal Ecology 73:469–477.

Prather, C. M., et al. 2013. Invertebrates, ecosystem services and climate change. Biological Reviews 88:327–348.

Pyke, G. H. 2015. Understanding movements of organisms: It's time to abandon the Levy foraging hypothesis. Methods in Ecology and Evolution 6: 1–16.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reynolds, A. M., H. B. C. Jones, J. K. Hill, A. J. Pearson, K. Wilson, S. Wolf, K. S. Lim, D. R. Reynolds, and J. W. Chapman. 2015. Evidence for a pervasive 'idling-mode' activity template in flying and pedestrian insects. Royal Society Open Science 2:150085.

Rzanny, M., and W. Voigt. 2012. Complexity of multitrophic interactions in a grassland ecosystem depends on plant species diversity. Journal of Animal Ecology 81:614–627.

Saska, P., W. van der Werf, L. Hemerik, M. L. Luff, T. D. Hatten, and A. Honek. 2013. Temperature effects on pitfall catches of epigeal arthropods: a model and method for bias correction. Journal of Applied Ecology 50:181–189.

Scheller, H. V. 1984. Pitfall trapping as the basis for studying ground beetle (Carabidae) predation in the spring barley. Danish Journal of Plant and Soil Science 88:317–324.

Schuldt, A., et al. 2015. Multitrophic diversity in a biodiverse forest is highly nonlinear across spatial scales. Nature Communications 6:10169.

Siemann, E., D. Tilman, and J. Haarstad. 1999. Abundance, diversity and body size: patterns from a grassland arthropod community. Journal of Animal Ecology 68:824–835.

Spence, J. R., and J. K. Niemelä. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. Canadian Entomologist 126: 881–894.

Thomas, C. F. G., N. J. Brown, and D. A. Kendall. 2006. Carabid movement and vegetation density: implications for interpreting pitfall trap data from splitfield trials. Agriculture Ecosystems & Environment 113:51–61.

Thomas, C. F. G., L. Parkinson, and E. J. P. Marshall. 1998. Isolating the components of activity-density for the carabid beetle *Pterostichus melanarius* in farmland. Oecologia 116:103–112.

Topping, C. J., and K. D. Sunderland. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. Journal of Applied Ecology 29:485–491.

Wallin, H., and B. S. Ekbom. 1988. Movements of carabid beetles (Coleoptera, Carabidae) inhabiting cereal fields – a field tracing study. Oecologia 77:39–43.

Wang, X. W., J. Muller, L. L. An, L. Z. Ji, Y. Liu, X. G. Wang, and Z. Q. Hao. 2014. Intra-annual variations in abundance and species composition of carabid beetles in a temperate forest in Northeast China. Journal of Insect Conservation 18:85–98.

Woodcock, B. A. 2005. Pitfall trapping in ecological studies. Pages 37–57 *in* S. R. Leather, editor. Insect sampling in forest ecosystems. Blackwell Publishing, Oxford, UK.

Work, T. T., C. M. Buddle, L. M. Korinus, and J. R. Spence. 2002. Pitfall trap size and capture of three taxa of litter-dwelling arthropods: implications for biodiversity studies. Environmental Entomology 31:438–448.

Zhao, Z. H., P. J. Shi, C. Hui, F. Ouyang, F. Ge, and B. L. Li. 2013. Solving the pitfalls of pitfall trapping: a two-circle method for density estimation of ground-dwelling arthropods. Methods in Ecology and Evolution 4:865–871.

Zurell, D., et al. 2010. The virtual ecologist approach: simulating data and observers. Oikos 119:622–635.

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